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SYNTHETIC PINK-EYED SELF WHITE GUINEA-PIGS[1]

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INTRODUCTION

In the fall of 1914 Professor W. E. Castle kindly sent to the Department of Experimental Breeding, University of Wisconsin, five guinea-pigs representing some of the rarer color varieties, suggesting that their genetic make-up be studied independently. These animals were subsequently turned over to the writer for investigation. During the winter two of them died without offspring and hence only three were left the following spring. Two of these proved to be what has been called by Castle red-eyed agoutis and the third was a "pink-and-red-eyed" tortoise. The factors involved in the production of these animals will be described below in more detail.

Castle (1914) had already described the different factors found in these animals and had given some indication of their relationships to other factors. At this time he stated that red-eyed was allelomorphic to albinism, and that pink-eyed was recessive to the usual dark-eyed condition. In 1915 Wright showed that red-eyed formed an allelomorphic series with albinism and dilute and intense pigmentation. This made the account of the relationships of the factors fairly complete.

At about this time it occurred to the writer that with the proper combination of the newly described factors and other factors it should be possible to produce an animal which to all appearances would be an ordinary albino, but entirely different genetically from what have hitherto been known as albinos. Matings were immediately started with this in view, but since there were only three animals to work with at the start progress was necessarily slow at first.

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[1] Papers from the Department of Genetics, Wisconsin Agricultural Experiment Station, No. 13. Published with the approval of the Director of the Station.

In the meantime Detlefsen (1916) had described some pink-eyed white mice carrying the color factor. He believed they were due to the combination of the dominant self white condition and the pink-eyed, but in his paper this was not fully demonstrated.

Castle (1916) refers to two pink-eyed white guinea-pigs, presumably albinos, which were born to pigmented parents. The male parent was tested with true albinos, but all of the eleven offspring obtained were pigmented. Castle therefore supposes that the two pink-eyed white offspring were not true albinos, but "pink-and-red-eyed" animals lacking the factor for the extension of black or chocolate pigment. This is undoubtedly the correct explanation, as the evidence presented in this paper will demonstrate. Castle, however, must have discarded his pink-eyed whites before he realized their importance since he makes no mention of testing them genetically.

Before going into further detail it may be well to describe briefly the various factors directly concerned in the production of the pink-eyed self whites. Some of those indirectly concerned are also described in order to give the proper orientation.

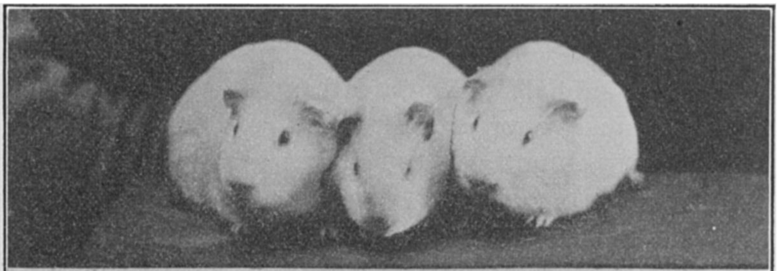
Description of Factors

B, the factor for black pigmentation. When unmodified by other factors black pigment is found only in the eyelids, mammae, external genitals and the skin of the ears and feet.

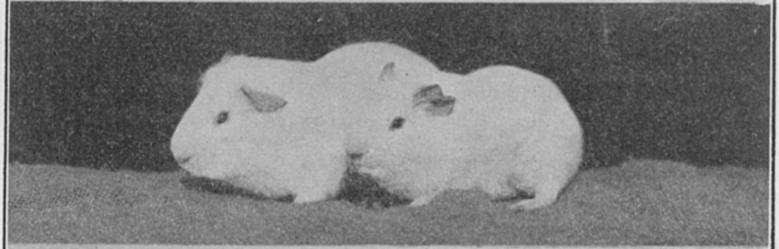
b, the factor for chocolate (or brown) pigmentation.

E, the factor for extension of black or chocolate throughout the pigmented part of the coat. The unpigmented parts are of course white.

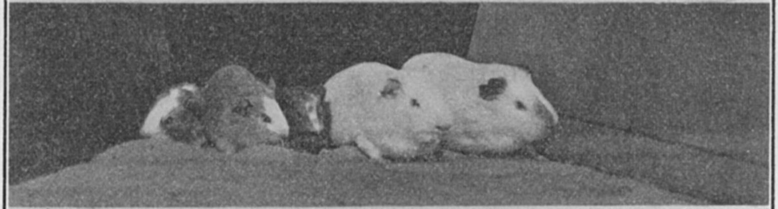
e^p, the partial extension factor. This factor causes black or chocolate to be only partially extended and therefore to appear in blotches, the remainder



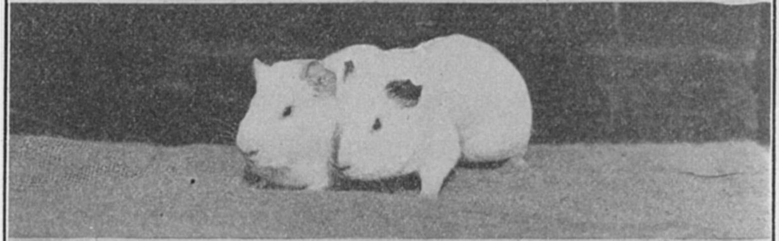
1 ♀1118.1 ♀1866.2 ♂1830.1



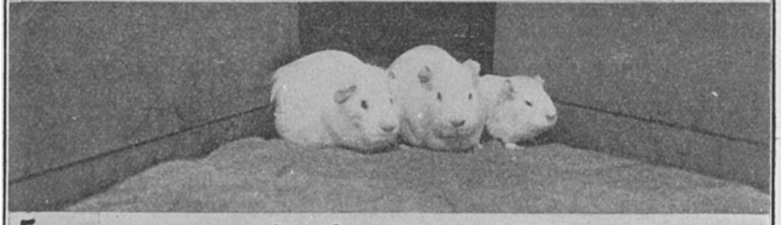
2 ♂849.1 ♂1258.1



3 Litter 1514 ♂1202.1 ♀1171.3



4 ♂1202.1 ♀1171.3



5 ♀1118.1 ♂1202.1 ♂1587.1

of the pigmented part being red. Guinea-pigs spotted black and red in this manner are commonly known as tortoises.

e, the non-extension of black or chocolate. In this case black or chocolate are found only in the places mentioned under *B*, *i. e.*, in the eyelids, etc. *E*, e^p and *e* form an allelomorphic series (Ibsen, 1916). They are given in the order of their dominance.

C, intense pigmentation.

C_d, dilute pigmentation. Yellow is dilute red.

C_r, red-eyed or non-yellow. In a C_r animal red (or yellow) is never present in the coat and black or chocolate are somewhat dilute. Owing to the absence of red the amount of pigment in the eyes is decreased, thereby partially allowing the blood to show through. It is because of this reddish tint to the eyes that they have been called red-eyed by Wright (1915). However, it seems more proper to call them non-yellows since the absence of yellow in the coat is the more general and striking effect produced by the factor. A C_r tortoise is therefore black-and-white because the red spots of the ordinary tortoise are here absent. An *eC* animal is a self red, but an animal with the composition eC_r is a self white, owing to the absence of red pigment. Such an animal will be referred to in the text as a "non-extended (*e*) non-yellow (C_r)."

FIG. 1. From left to right: ♀ 1118.1, a pink-eyed non-extended non-yellow; ♀ 1866.2, an albino carrying both black (*B*) and the extension factor (*E*); ♂ 1830.1, an albino lacking both black and extension and therefore *be*. Owing to the pink color of the skin of the ears of ♀ 1118.1 and ♂ 1830.1, and also because of the direction of the light, causing them to cast shadows, the ears appear darker than they really are. The pink eyes also appear dark.

FIG. 2. Guinea-pig, ♂ 849.1 is a *bb* dark-eyed non-extended non-yellow. ♂ 1258.1 is a dark-eyed non-extended non-yellow carrying black (*B*).

FIG. 3. Guinea pigs ♂ 1202.1, a pink-eyed non-extended non-yellow (ppC_rC_rce), ♀ 1171.3, an albino heterozygous for partial extension (*ep*), and three of their offspring, litter 1514.

FIG. 4. A nearer and clearer view of ♂ 1202.1 and ♀ 1171.3, already shown in Fig. 3.

FIG. 5. Guinea-pigs ♂ 1202.1 and ♀ 1118.1, both pink-eyed non-extended non-yellows and one of their 24 offspring, ♂ 1587.1, also a pink-eyed non-extended non-yellow.

The C_r factor has been described in some detail because it plays an important part in the production of the synthetic pink-eyed self whites. C and C_d are dominant to C_r, while it in turn is dominant to C_a.

C_a, albinism. Albino guinea-pigs generally tend to have some pigmentation on the nose, ears and feet. This varies in amount depending on the other factors present. A *be* albino is almost if not quite devoid of pigment (♂1830.1, Fig. 1), while a *BE* albino is heavily pigmented at its extremities (♀1866.2, Fig. 1). In all cases, however, the eyes are pink and the greater part of the coat is white.

P, dark-eyed.

p, pink-eyed. The eyes are as pink as those found in albinos. Black (*B*) or chocolate (*b*) are also affected, becoming quite dilute, while red is unaffected.

It will be seen from the description of the factors given above that if we can obtain an animal which is a non-extended non-yellow, eC_r, and therefore a self white, and which in addition is *pp*, or pink-eyed, we shall have a pink-eyed self white (eC_rp), which is not an albino in the ordinary sense of the word as applied to guinea-pigs, but which nevertheless to all appearances in an albino (see ♀1118.1, Fig. 1). There is one difference, however. Albinos vary considerably in the amount of pigment in the ears, nose and feet depending on whether E, e^p, or B are present or absent. The synthetic pink-eyed self whites on the other hand cannot carry E or e^p, but may carry B. The pink-eyed factor (p) dilutes black pigment (B) to such an extent that it is impossible to tell by the appearance of the animal whether or not black is present. All the synthetic pink-eyed self whites are therefore a pure white and fulfil the guinea-pig fancier's requirements for a good albino better than most true albinos do.

BREEDING OPERATIONS

As previously stated there were three animals with which to begin breeding operations in the production of the synthetic pink-eyed self whites. These were two non-yellow agoutis, ♂ 360.1 and ♀ 361.1, and a pink-eyed non-yellow tortoise, ♀ 363.1. By various test matings these were proven to be of the following gametic compositions: ♂ 360.1, $AaPpC_rC_re^pe^p$,[2] ♀ 361.1, $AaPPC_rC_re^pe^p$, and ♀ 363.1, $aappC_rC_re^pe^p$. It will be seen that all three were homozygous for e^p, the factor for the partial extension of black or chocolate. On this account it would be impossible by mating the animals together to produce the pink-eyed self whites since the desired animals must lack the extension factor and therefore be ee.

What seemed the best method of procedure was to mate ♀363.1 ($ppC_rC_re^pe^p$) to a self red ($PPCCee$), and then to inbreed the F_1's ($PpCC_re^pe$). These all looked like ordinary tortoises. Since this was a tri-hybrid cross and since the desired animals were to be homozygous recessives, it would theoretically be necessary to have 64 offspring for the production of one of the desired type. This proved to be a very slow process and was finally discarded in favor of other less methodical matings, which were more rapid in their results. The most successful will be described in some detail.

A heterozygous tortoise ♂ 572.1, of the composition $PpCC_re^pe$ obtained by mating ♂ 360.1 to a self red, was mated to a yellow-and-white female, 629.3, carrying albinism (PPC_aC_aee). One of their offspring, ♂ 849.1 (Fig. 2), was at first mistaken for an albino, but more careful examination proved him to be a dark-eyed non-extended non-yellow. The reason for mistaking him for an albino was that he did not carry black (B).[3] His gametic composition turned out to be PpC_rC_aee. He was mated to a pink-eyed tortoise, ♀734.2,[4] whose composition judging by her offspring, must have been $ppC_dC_re^pe$. This cross may be represented as follows:

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[2] A is the factor for agouti.

[3] In a dark-eyed non-extended non-yellow (PeC_r) the presence or absence of black (B) is as easily detected as it is in an albino or a self red. In Fig. 2 ♂ 1258.1 carries black while ♂ 849.1 does not. In addition to having much lighter colored extremities a bb non-extended non-yellow also has much pinker eyes than one which carries black. For this reason it may be mistaken for an albino.

	♂ 849.1	×	♀ 734.2
	PpC_rC_aee		$ppC_dC_re^pe$
Gametes	PC_re		pC_de^p
	PC_ae		pC_de
	pC_re		pC_re^p
	pC_ae		pC_re

Offspring		Obtained
$PpC_dC_re^pe$ $PpC_dC_ae^pe$	Dark-eyed tortoise	1
$ppC_dC_re^pe$ $ppC_dC_ae^pe$	Pink-eyed tortoise	2
PpC_dC_ree PpC_dC_aee	Dark-eyed self-yellow	2
ppC_dC_ree ppC_dC_aee	Pink-eyed self-yellow	2
$PpC_rC_re^pe$ $PpC_rC_ae^pe$	Dark-eyed non-yellow tortoise	2
$ppC_rC_re^pe$ $ppC_rC_ae^pe$	Pink-eyed non-yellow tortoise	0
PpC_rC_ree PpC_rC_aee	Dark-eyed non-extended non-yellow	1
ppC_rC_ree ppC_rC_aee	*Pink-eyed non-extended non-yellow*	2
Total		12

It will be seen that according to expectation there should be equal numbers of 8 different phenotypes. The 12 offspring actually obtained are remarkably close to expectation.

At the time this cross was made the gametic composition of the mother, ♀734.2, was not definitely known. When, therefore, the two pink-eyed non-extended non-yellows were born one could not be certain that they were not just ordinary albinos. The only definite method

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[4] Ancestry of ♀ 734.2:

♀ 734.2, $ppC_dC_re^pe$	♂ 346.1, $PpC_dC_re^pe$	♂ 179.1, $PPCC_dee$
		♀ 363.1, $ppC_rC_re^pe^p$
	♀ 549.3, $PpC_rC_re^pe^p$	♂ 360.1, $PpC_rC_re^pe^p$
		♀ 361.1, $PPC_rC_re^pe^p$

to test this was to mate them to true albinos, and this was accordingly done.

One of these animals, ♀1118.1 (Figs. 1 and 5), mated to an albino,[5] ♂596.3 (PPC_aC_aee), had 4 dark-eyed non-extended non-yellow offspring and 2 albinos. This would make her composition ppC_rC_aee and the cross may be represented as follows:

♂596.3 × ♀1118.1
PPC_aC_aee ppC_rC_aee
Gametes: $\left\{ PC_ae \right.$ pC_re
pC_ae
Offspring: PpC_rC_aee, dark-eyed non-extended non-yellow;
PpC_aC_aee, albino.

The other animal, ♂1202.1 (Figs. 3, 4 and 5), was mated to an albino (♀1171.3, Figs. 3 and 4) of the composition $PPC_aC_ae^pe$. There were 12 offspring. Of these 6 were dark-eyed non-yellow tortoises and the other 6 were dark-eyed non-extended non-yellows (see litter 1514, Fig. 3). This would indicate that ♂1202.1 was of the composition ppC_rC_ree, and the cross would be as follows:

♂1202.1 × ♀1171.3
ppC_rC_ree $PPC_aC_ae^pe$
Gametes: $\left\{ pC_re \right.$ PC_ae^p
PC_ae
Offspring: $PpC_rC_ae^pe$, dark-eyed non-yellow tortoise;[6]
PpC_rC_aee, dark-eyed non-extended non-yellow.

It will thus be seen that the two pink-eyed non-extended non-yellows were not of the same composition, the male, 1202.1 being homozygous for C_r, while the female, 1118.1, was C_rC_a. This is what one might expect by reason of their parentage.

According to expectation, these pink-eyed non-extended non-yellows when bred together should have nothing but pink-eyed non-extended non-yellow offspring. Thus:

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[5] The albinos used in these test matings were unquestionably homozygous dark-eyed (PP) since they came from stock that has never been known to carry the pink-eyed factor (p).

[6] These dark-eyed non-yellow tortoises as well as the dark-eyed non-extended non-yellows are being inbred, and the results from these matings will be reported at some future date.

	♂ 1202.1 ×	♀ 1118.1
	ppC_rC_ree	ppC_rC_aee
Gametes:	pC_re	pC_re pC_ae
Offspring:	ppC_rC_ree ppC_rC_aee	pink-eyed non-extended non-yellows.

The mating has been made and thus far there have been 24 offspring, all of them pink-eyed non-extended non-yellows (see Fig. 4). Some of these offspring are being tested by being mated to albinos, but as yet their composition with respect to the presence of albinism is not definitely known. It may be of interest to mention that one of them when mated to a *PPEE* albino had one dark-eyed *self black* offspring. The other two offspring in the same litter were black-and-white, due to the fact that neither parent was homozygous for entire pigmentation (*S*).[7]

DISCUSSION

In most domesticated mammals an albino, as ordinarily understood by breeders, is a completely self white animal with pink eyes. Albino rabbits are of this type. In addition there is the Himalayan variety which also has pink eyes, but the coat instead of being entirely white is pigmented at the animal's extremities. This condition is dominant to albinism and recessive to the fully pigmented condition, thus forming part of an allelomorphic series (Sturtevant, 1913). Guinea-pig fanciers also have what they call a Himalayan variety. Here, however, the genetic relationship differs from that found in rabbits. Himalayan guinea-pigs are undoubtedly true albinos carrying the factor for black (*B*) and the extension factor (*E*) which extends the black. The presence of these two factors tends to make the extremities heavily pigmented.

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[7] An *S* animal is entirely pigmented, while one that is *ss* shows some white spotting and is therefore not entirely pigmented. In this connection it may be of interest to note that in a non-yellow tortoise the white spotting may be due to two different causes, (1) because of the non-yellow factor (C_r) the yellow of the ordinary tortoise is here white, and (2) if the animal is *ss* it will show some white spotting on this account also.

The albino guinea-pig, according to the fanciers' standard, should be as completely white as the albinos of other species. This, however, has never been entirely attained, even though much selection has been practised. Albinos most nearly approaching the standard lack both black and extension factor and are therefore *eb*. When mature they ordinarily show, nevertheless, a lightly pigmented rim along the edges of the ears. The synthetic pink-eyed whites, produced as explained in the earlier part of this paper, are, on the other hand, pure white, and they therefore satisfy the fanciers' standard in this respect. They would meet his desires, furthermore, in that they breed true for this character.

There are other means besides those already mentioned whereby pink-eyed self white guinea-pigs could be produced which would satisfy the fancier's standard. One method would be to combine a self white condition described by Castle (1905) with the pink-eyed. Self whites of this type, however, do not breed true. Very frequently they throw spotted offspring. They seem to be merely an extreme form of white spotting, all of the animal being unpigmented except the eyes. Pink-eyed self-whites of this type would necessarily on this account be very unstable in the transmission of their coat character.

Another method would be to produce a "pink-eyed" (*pp*) albino. The pink-eyed factor in this case would cause the pigmentation ordinarily found in albinos to become invisible. We have produced an animal of this type. When mated to pink-eyed it had nothing but pink-eyed offspring, and when mated to albinos it had only albino offspring. It was pure white in color.

It seems quite probable that synthetic pink-eyed self whites may also be produced in rats. Castle (1914) has already described yellow varieties and pink-eyed varieties, and Whiting (1916) has stated that the non-yellow factor has been found in some animals.

In conclusion it may be said that we have furnished one more proof of the fact that the phenotypic appearance of an animal may entirely mislead one as to its gametic composition. The synthetic pink-eyed self white guinea-pig may also serve another purpose. By proper matings an animal can be produced which carries all the known recessive color factors in guinea-pigs except albinism, and animals of this type should be most useful in determining the possible linkage relations between the factors.

LITERATURE CITED

Castle, W. E.
1905. Heredity of coat characters in guinea-pigs and rabbits. Carnegie Institution of Washington, Publication No. 23, 78 pp. 5 pls.
1914. Some new varieties of rats and guinea-pigs and their relation to problems of color inheritance. Amer. Nat., Vol. 48, pp. 65–73.

Castle, W. E., and Sewall Wright.
1916. Studies of inheritance in guinea-pigs and rats. Carnegie Institution of Washington, Publication No. 241, 192 pp.

Detlefsen, J. A.
1916. Pink-eyed white mice, carrying the color factor. Amer. Nat., Vol. 50, pp. 46–49.

Ibsen, H. L.
1916. Tricolor inheritance. I. The tricolor series in guinea-pigs. *Genetics,* Vol. 1, pp. 287–309.

Sturtevant, A. H.
1913. The Himalayan rabbit case with some considerations on multiple allelomorphs. Amer. Nat., Vol. 47, pp. 234–238.

Whiting, P. W.
1916. A new color variety of the Norway rat. *Science,* N. S., Vol. 43, p. 781.